ON THE EVOLUTION OF HUMAN FIRE USE

by

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STATEMENT OF DISSERTATION APPROVAL

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ABSTRACT

Humans are unique in their capacity to create, control, and maintain fire. The evolutionary importance of this behavioral characteristic is widely recognized, but the steps by which members of our genus came to use fire and the timing of this behavioral adaptation remain largely unknown. These issues are, in part, addressed in the following pages, which are organized as three separate but interrelated papers.

The first paper, entitled "Beyond Firestick Farming: The Effects of Aboriginal Burning on Economically Important Plant Foods in Australia's Western Desert," examines the effect of landscape burning techniques employed by Martu Aboriginal Australians on traditionally important plant foods in the arid Western Desert ecosystem. The questions of how and why the relationship between landscape burning and plant food exploitation evolved are also addressed and contextualized within prehistoric demographic changes indicated by regional archaeological data.

In the second piece, "The Pyrophilic Primate Hypothesis," recent paleoenvironmental reconstructions and models from Optimal Foraging Theory are used to construct an evolutionary scenario of human fire dependence during the Plio-Pleistocene transition in Africa ~2.5-2.0 million years ago. The foraging benefits identified in this fire-altered habitat are linked to our evolutionary ancestors'

transformation into a genus of active pyrophiles whose dependence on fire for survival contributed to its expansion out of Africa.

The final paper, "On the Archaeological Signature of Human Fire Use: Analyses, Interpretations, and Implications for Understanding the Evolution of Pyrotechnic Behaviors," reviews recent debates about the timing of anthropogenic fire based on archaeological data. The efficacy of archaeological markers in constructing hypotheses of prehistoric human fire use is assessed by comparing archaeological fire signatures, or lack thereof, in Europe and North America.

Each paper constitutes one component of a broader intellectual goal: to show that genus *Homo* is a primate adapted to and dependent upon fire for its survival and reproduction. Our genus' active pyrophilia is a unique trait, and it is hoped that the following pages contribute to a better understanding of how, when, and why this trait evolved.

For my family
and
Nyaperu

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CHAPTER 1

BEYOND FIRESTICK FARMING

1.1 Abstract

Human foragers frequently interact with their environment through the controlled application of fire to the landscapes in which they live. This can shape habitats, influence resource availability, and potentially transform entire ecosystems. We present results from a long-term research project among the Martu Aboriginal People of Australia's Western Desert examining the effects of anthropogenic burning on traditional plant food populations. We have previously reported that the immediate increases in women's hunting return rates explain the timing and size of Martu burns, which result in vegetational mosaics at a distinctly finer scale from that produced by lightning fires. Here we report the successional consequences for plant communities and consider implications for subsequent resource use. Our data indicate that the immediate foraging returns from postburn burrowed game hunting are unavailable until spinifex (*Triodia* spp.) regrowth has reached sufficient density to once again carry a fire, but that the return rates available from useful food plants increase in the intervening successional regrowth period. This interannual pattern provides important insights into arid zone foraging strategies, and the colonization process of Australia's deserts.

1.2 Introduction

One of the most characteristic practices associated with Aboriginal Australians is the widespread use of frequent landscape burning. The impact of fire on Australian biodiversity is widely acknowledged (e.g., Bowman 1993, 1998; Bowman and Latz 1993; Bradstock et al. 2002; Latz 1995) yet an understanding of anthropogenic burning regimes remains limited (Bowman 1998; Bradstock et al. 2002). Australian Aborigines have an active rather than passive relationship with their environment, leading many researchers to argue that Aboriginal burning practices are designed to ensure the availability of economically important plants and animals by both increasing general biodiversity and stabilizing the populations of specific resources (e.g., Gould 1971; Burbidge et al. 1988; Burbidge and McKenzie 1989; Jones 1969, 1980; Nodvin et al. 1990; Russell-Smith and Bowman 1992; Russell-Smith et al. 1997a,b; Yibarbuk et al. 2001), often with significant environmental impacts (Burrows and Christensen 1990; Burrows et al. 2000, 2006; Haydon et al. 2000a,b).

In fire-prone arid Australia, the grasses, forbs, fruit, and insects that quickly colonize burned areas following seasonal rain are important food resources for humans and the animals they hunt, including large and small macropods (*Macropus, Wallabia,* and *Petragale* spp.), emu (*Dromaius novaehollandiae*), and bustard (*Ardeotis australis)* (Latz 1995). Since regular burning increases edible forage for game animals and facilitates flushing them during hunts (Finlayson 1936), many anthropologists have focused on the relationship between landscape burning and mobile game hunting (e.g., Gould 1971; Jones 1975, 1980; Kimber 1983; Bowman et al. 2001). We have previously reported data showing that instead, Aboriginal burning practices in the

Western Desert of Australia can be explained by the immediate foraging benefits reaped by Martu women during seasonal burrowed game hunts (Bliege Bird et al. 2008, 2012, 2013; Bliege Bird and Bird 2008; Bird et al. 2005, 2003). Burning off spinifex ground cover in sandplain landscapes immediately increases search efficiency for Martu women by exposing the holes and tracks of target species such as goanna (*Varanus gouldii*), skink (*Tiliqua multifasciata*), python (*Aspidites* spp.), and feral cat (*Felis silvestris*) that are otherwise obscured by old-growth spinifex.

This increased visibility improves *wana* (digging stick) hunters' ability to find, read, and interpret the subtle clues that indicate whether a den is occupied and therefore likely to be productive. Once holes with a higher probability of being occupied are identified, Martu *wana* hunters carefully probe the ground surrounding a hole to find the exact location of the prey within the den. Once this area is isolated, the prey is extracted from the den by manual digging made easier by the removal of groundcover that would otherwise impede this process. Systematically employing small-scale, low-intensity burning during burrowed game hunts allows *wana* hunters to more efficiently and *predictably* encounter, pursue, and process burrowed prey. Most of Martu broadcast burning is conducted during cool-dry season hunts: by clearing a large patch of late successional spinifex, foragers increase net hunting return rates 62 fold (Bliege Bird et al. 2013, table 2). In the summer, when varanid lizards are pursued by tracking, access to ground burned earlier in the season is critical: returns are lower with more plant cover as tracks become more difficult to see (Bliege Bird et al. 2013).

Burning, then, provides short-term foraging benefits by reducing the amount of time allocated to search and postencounter handling activities. These short-term benefits,

especially those that improve postencounter handling effort, effectively change the prey type of target species by increasing the profitability of prey items as less time and energy is required for extractive activities after a burning episode. These hunting benefits, however, are only available during a limited period of time following a burn. Return rates for hunting burrowed game rapidly decline as the resource patch is depleted (Bliege Bird et al. 2013), and as we document here, several years must pass for spinifex cover to regrow to a point it can once again provide cover for burrowing animals and carry a fire.

There are also longer-term foraging benefits that accrue as an effect of these burning practices. Large animals may be attracted to the herbaceous plants appearing after a burning episode (Bowman et al. 2001; Jones 1969), and plants targeted and consumed by human foragers emerge in postignition landscapes as well. The contemporary use of fire by Martu Aboriginal Australians to modify the landscape of their Western Desert homelands provides a unique opportunity where a "natural experiment" allows us to measure both immediate and subsequent effects of anthropogenic burning on the foraging landscape. Here, we present a quantitative analysis of the effects of anthropogenic fire on selected plant foods and consider some consequences of the resulting temporal effects on foraging opportunities.

Identifying the immediate and long-term foraging benefits produced by Martu pyrogenic landscape alteration is particularly relevant to understanding changes in diet and arid zone land use patterns archaeologically indicated during the mid- to late Holocene (Smith and Ross 2008). The archaeological presence of grinding technology ~1.5kya reflects the relatively recent inclusion of resources with high processing costs,

especially seed grasses, in the diet of hunter-gatherers inhabiting Australia's deserts. The data presented here indicate that the increased availability of edible seed-bearing grasses on the landscape is a consequence of anthropogenic burning. We contextualize this foraging benefit within scenarios of rapid population growth in the Australian arid zone during the Holocene to how and why the aforementioned dietary changes and in land-use intensification likely evolved.

1.3 Ethnographic and Ecological Setting

The term Martu (also Mardu, Mardujarra) refers to the roughly 800 traditional Aboriginal owners of estates surrounding Lake Disappointment, the Rudall River, and the Percival Lakes in the northwest section of the Australian Western Desert. The members of the eight dialect-named groups in this region use "Martu" (meaning "man" or "people") to refer to themselves collectively (Tonkinson 1991 p. 12), and much has been written about their social organization, history, religion, gender roles, and politics (Tonkinson 1974, 1990, 1991, 2007). For a few Martu, contact with Europeans began early in the 1900s, but direct interaction remained limited or nonexistent for many families until they were drawn into the early government depot and mission of Jigalong and nearby pastoral stations as a result of slow depopulation and prolonged drought in the mid-1960s (Tonkinson 1974). At least five flexible bands of predominantly Manyjilyjarra and Warnman speakers, some of whom were eventually cleared from their homelands in preparation for joint British-Australian missile tests, ranged throughout the McKay Range-Rudall River and Percival Lakes-northern Canning Stock Route regions during this time (Peterson and Long 1986:116-121). Others remained on their traditional homelands until 1966-1967 when they were brought in by government

patrols or walked in on their own to rejoin their families in Jigalong (Davenport et al. 2005). During the period spanning 1940 to 1967, many Putijarra, Kartujarra, Kurajarra, and Pijarkarli dialect speakers also began settling in and around the European settlements of Nullagine, Marble Bar, and Balgo. While many Martu stayed in these communities, by the mid-1980s, several families (primarily Manyjilyjarra, Kartujarra, and Warnman-speakers) returned permanently to their traditional desert homelands. By 1986, they had established two permanent outstation camps, Punmu and Parnngurr, in the newly designated Rudall River National Park, with the outstation of Kunarwarritji at Well 33 on the Canning Stock Route established a short time later (Tonkinson 1991:174-178).

Resettlement to these communities in the mid-1980s meant returning to a hunting and gathering economy that incorporated traditional landscape burning practices (Veth and Walsh 1988; Walsh 1990). While reliance on wild foods has diminished somewhat as a result of increased access to commercially processed foods and reliance on government-sponsored economic support, many of the 100 or so people living in Parnngurr continue to forage within 50km of the community on a more or less daily basis. Foraging excursions to extended camps at distant locales are also common during the cool-dry *Wantajarra* season (May to August) when most anthropogenic burning occurs.

The use of fire is an important component of Martu foraging and has an observable impact on the desert landscape. This is well-represented in Tonkinson's (1991:51) description of Martu burning practices:

> Mardu burning activities provide the most telling evidence of their modification to the landscape. The ground is cleared by fire; then, when rain falls, new plants

> grow on the burnt patch. For example, the Mardu burn spinifex to "bring up" grasses, herbs, and bush tomatoes that are more useful as food resources, since spinifex seeds are unreliable and laborious to harvest. Many of these early colonizer species provide bushfood for Mardu and fresh growth for game (Latz 1982, Walsh 1990). As the burnt patch ages, other plants replace the early species. The small fires lit by Mardu as they travel thus result in a mosaic of plant communities, which are an important feature of desert ecosystems.

This account shows how burning dramatically alters the spinifex (*Triodia* spp.) dominated landscapes of Martu country. The relationship between fire and landscape vegetation is complex: fires fueled by spinifex ground cover initially act as a destructive force that removes plant life from the landscape. This increases return rates for Martu women, reducing both search and pursuit time for the prey they target as holes and tracks are exposed. The high hunting return rates they earn immediately following a burn then fall as game is extracted from the productive holes exposed within the newly burned area. Even as prey species return with the postburn successional plant regrowth, the high rates associated with firing will be unavailable until the spinifex cover necessary to carry a flame is reestablished. Yet this process allows new communities of plants that serve as food resources to proliferate after rainfall. In the years following a burning episode, populations of fruit (*Solanum* spp.) and seed grasses (e.g., *Eragrostis, Dysphania*) which are important components of traditional Martu diets decline as spinifex again recolonizes and dominates the landscape (Latz 1995:10). Because the composition of plant communities changes over time, the opportunity for burning as well as the presence or absence of certain important plant foods will be closely tied to specific stages of regrowth.

1.4 Methods

We collected two interrelated sets of data to obtain a more complete picture of the long-term effects of Martu burning on arid zone plant life: (1) the precise location of fires lit by Martu during foraging excursions, and (2) systematic plant survey data collected in and around these burned areas in the following years.

1.4.1 Ignition Point Locations

During extended periods of ethnographic field work in 2000, 2001, and 2002, we recorded the locations of Martu fires during "day hunts" in the general vicinity of Parnngurr and on extended foraging trips away from the Outstation communities as GPS waypoints on a professional-grade, handheld GPS unit with ± 3 meter accuracy. An observer recorded the location, date, name of the individual lighting the fire, prevailing wind direction, direction of fire travel, estimated age of the spinifex being burned, and name of the nearest traditionally recognized landmark (e.g., "Tiwa bore," "Winukurujunu creek," "Parpulyi rockhole," etc.) as fires were lit during foraging. The exact date and location of these fires allowed for a simple yet accurate assessment of the age of vegetative regrowth in the following years. The location of a December 2002 burn, for example, showed six months of regrowth in June of 2003, and a year and a half of regrowth in June 2004. Because burn locations were recorded over the span of three years (2000, 2001, 2002), the corresponding record of known vegetative regrowth in burned areas encompasses a range of up to five years in age.

1.4.2 Plant Surveys

We used burn locations as the starting point of systematic ecological surveys undertaken in 2003 and 2004 involving a combination of ten-meter wide, five-kilometer long straight-line transects, systematically placing five x five meter sample plots along each transect. After relocating known ignition points with the GPS receiver, we projected a point location five kilometers away in a randomly selected direction and assigned it a waypoint, projecting another waypoint five kilometers away 180 degrees in the opposite direction, resulting in a total transect length of ten kilometers centered on the known ignition point. Except when prohibited by impassable terrain, two researchers walked each five kilometer transect leg to the end waypoint, recording the number and species of ethnographically-known plants traditionally exploited by Martu foragers, including tubers (*Vigna lanceolota)*, fruits (*Solanum* spp.), seed grasses (*Eragrostis* spp.), and nectar-producers (*Grevillea* spp., *Hakea*, and *Leptosema chambersii*). We chose these plants specifically because they represent components of both traditional and contemporary Martu diets (Walsh 1990).

Changes in burn/regrowth age were noted while walking the transects and assigned a waypoint if the change was continuously observable for 100 meters after initial indications of entering a different age of postignition plant regrowth. Such change is typically indicated by a measurably significant difference in the diameter, height, and color of spinifex hummocks, and the extent to which it dominates groundcover. We measured spinifex diameter in all burn/regrowth landscapes to estimate the age of the burn, and confirmed or modified this estimated age after consulting with Martu informants. Burn/regrowth ages older than those falling within the known burn ages

were assigned categorical ages of five to ten (5-10) years, and ten plus (10+) years based on spinifex diameter, which occasionally reached a width of over two meters in the areas of oldest regrowth. When a fresh burn (indicated by the presence of particulate surface ash) was encountered during transects, its location was assigned a GPS waypoint and given a date designated by the month and year it was observed since the exact ignition timing was unknown.

Changes in ecozone were also noted and marked with waypoints during transect walking. Six ecozones were operationally defined loosely following Latz's (1995) description of Central Desert plant communities: spinifex-dominated ***sandplains*** and ***dunes***; ***rocky outcrops*** with little or no soil formation; vegetation communities unique to the ***watercourse margins*** of both permanent and ephemeral water sources; and three woodland zones, including ***eucalypt-dominated woodlands, mulga-dominated woodlands,*** and ***acacia-dominated shrublands***. Ecozone transitions were noted in the transect log on initial observation, and assigned a waypoint if the transect line continued through the ecozone for 100 meters.

Five by five (5x5) meter sample plots (quadrats) were deployed at specified intervals along each transect to increase the accuracy and precision of the ecological survey. Quadrats were placed at known ignition points that served as the start of each transect, and every 1000 meters from that starting point until reaching the end of the transect. This resulted in a minimum of five quadrats for each transect leg. Quadrats were also placed on the transect lines 100 meters after entering a new ecozone, and 100 meters after every observed change in estimated successional regrowth age. One corner of each quadrat was marked with a GPS waypoint, and its orientation (e.g., "southwest

corner," "northeast corner," etc.) noted in the transect record. Stem counts for all plants were conducted within each quadrat and the number and type of animal tracks and burrows noted (if present). The diameter, height, and color of spinifex were also recorded, providing an average of spinifex size for each burn/regrowth age. Plant counts from each transect and average spinifex diameters from quadrats were tabulated and their means assigned z-scores for standardized comparison.

1.5 Results

A total 173,220 meters were surveyed in 36 transect legs during the 2003 and 2004 field seasons. Because the majority of contemporary Martu foraging activity occurs within the ***sandplain*** and ***watercourse*** ecozones, the results from these areas are of particular interest. The data from these ecozones exhibit a generalized pattern of significant increases in the presence of economically important plant populations following a burning episode that continues until spinifex regrowth reaches the point that it is dense enough to carry a flame, around five years, at minimum, from a burn.

In ***sandplains*** (Figure 1.1), significant presence of fruit-bearing plants is observable very soon after a burning episode, as early as 6 months after ignition in the case of *Solanum centrale*. Observable peaks in populations of *Solanum chippendalei* occur roughly 1.5 years after ignition, and the presence of *Solanum ellipticum* is greatest in burns around 2.5 years old, with few if any fruit plants observed in burned areas older than 3 years. Seed grass (*Eragrostis* spp.) populations appear to increase steadily in sandplains after a fire, with the highest densities observed in burned areas that have undergone 2 to 3 years of regrowth. Like fruits, the presence of seed grasses sharply declines in burns older than 3 years, and is effectively absent from the sandplain

landscape 5 years after initial ignition.

Two plant species exploited for their nectar (*Grevillia eriostachya,* and *Leptosema chambersii*) appear to have very different responses to fire. Populations of *Grevillia eriostachya* are highest at 1 year and 2 to 3 years after a burn, with an apparent decrease in number at 2 years. This pattern can be explained by high densities of small, immature, *Grevillia* seedlings that emerge in the year following a fire. Many of these seedlings do not survive to reach maturity, resulting in the decrease in observable numbers at 2 years, but those that do survive reach peak densities at 2 to 3 years of regrowth. *Leptosema chambersii*, conversely, reaches its highest observable density from 3 to 5 years after a fire, with numbers declining after 5 years.

In the ***watercourse margin*** ecozone (Figure 1.2), tubers (*Vigna lanceolata)* proliferate almost immediately after a fire, and continue to do so for 2 years before numbers begin to dwindle. Increased numbers of seed grasses (*Eragrostis* spp.), however, do not become apparent until between 1 to 2 years after a fire, with growth peaking at 2 years and then declining. This pattern differs from that observed for seed grasses in the sandplain ecozone where populations decline in three, rather than two, years after a burning episode (Figure 1.1).

1.6 Discussion

Martu have many rationales for firing the landscape; systematic seasonal burning is a ritual imperative codified in Dreamtime Law to "clean up country" (Tonkinson 1991), an activity viewed by many Aboriginal peoples a means of "humanizing" the landscape (Head 1994). While some contemporary burning occurs for this reason, the vast majority of fires are set by women during hunts for burrowed prey in the cool-dry

Wantajarra season (Bird et. al. 2005; Bliege Bird et al 2005, 2008). These fires are set to reduce groundcover, which exposes burrows and immediately improves the efficiency and profitability of hunting activities.

The regrowth pattern of economically important plant resources, the greater part of which were observed in areas burned in the pursuit of burrowed game, show that burning also produces longer-term benefits. The data show that after a firing episode in the sand plain ecozone, *Solanum centrale* fruits are at peak availability in six months, *Solanum chippendalei* one year after that, and *Solanum ellipticum* in the following year. Seed grasses become increasingly abundant after the first year until populations begin to decline three years after a burn. While this pattern likely varies depending on the amount and timing of desert rainfall (see Latz 1995:23-26), the data indicate that burning generally stabilizes this relationship by altering the composition of plant communities that grow after burning removes the dominant spinifex understory. The stabilization of this inter-annual variability has important implications for foraging activity; burning during burrowed game hunts predictably encourages the growth of plants vital to survival, which become available after foragers reap the initial benefits of increased hunting efficiency.

Burning in this manner dramatically modifies the foraging landscape with respect to plant foods. This is apparent in the postburn landscape classification scheme employed by the Martu, which includes categories of relative foraging value correlating with each successional stage of plant regrowth following a fire:

1 *nyurnma*—a recently burned area with no plant regrowth typically exploited for burrowed prey

2 *waru-waru*—a landscape that is in the first successional stage of regrowth following a fire and seasonal rain, predominantly populated with herbaceous plants including some fruits

3 *nyukura*—a landscape in which herbaceous plants have matured with fruit and seeds available, but with spinifex increasingly abundant

4 *manguu*—a landscape where spinifex is present in densities sufficient for sustaining a fire, and in which herbaceous plants are present in very low densities or entirely absent, and

5 *kunarka*—a landscape dominated by very mature spinifex with little or no plant diversity which can take 10-20 years to develop, depending upon rainfall amounts.

The regrowth pattern observable in the data presented, in conjunction with the ethno-ecological landscape classification scheme employed by the Martu show both a spatial and temporal framework for available foraging options. As noted above, foraging opportunities in the form of burrowed game hunting decline rapidly after a nyurnma is created, leading to a period immediately following a burning episode in which burrowed game hunting is not profitable. A similar phenomenon can be seen in the spinifex and plant food regrowth pattern. There are "fallow" periods when plants with economic utility have yet to appear on the landscape, and again when they decline before the spinifex has reached a density that can sustain a fire.

Burning for burrowed game, then, alters both immediate and long-term foraging opportunities, constraining foraging options over time: immediate, high returns from hunting are available for a limited period; then foraging payoffs fall until plant regrowth

occurs following seasonal rainfall. Once the pattern of plant regrowth is established, economically useful plants become available for exploitation. Foraging options for these plant foods are subsequently eliminated by spinifex regrowth. High returns for hunting are not available until spinifex has grown enough to carry a fire.

This temporal sequence is a consequence of burning but not contingent upon any purposeful management of plant food resources. Rather, the positive impact of anthropogenic burning on traditionally exploited plant foods is a self-organizing *effect* of Martu landscape firing to reduce search effort and improve return rates while hunting burrowed game. This effect includes long-term increases in the availability of other resources, as well as the duration of waiting required until spinifex regrowth again allows burning. Understanding the interaction between anthropogenic burning and its effects on foraging opportunities can buttress colonization and population models of prehistoric Australia.

Archaeological and chronometric data suggest that movement inland from coastal areas occurred rapidly after human populations first arrived during the Pleistocene *circa* 46 kya BP (Allen and O'Connell 2008, 2003; O'Connell and Allen 2007, 2004). Material evidence of human behavior appears in the arid interior of the continent away from coasts and major river systems as early as 35-40 kya BP (Smith 2005), and continues until European contact. Despite an archaeological footprint indicating an early and continuous occupation of the region, evidence of seed processing technology does not appear until 1.5 kya (Smith & Ross 2008).

Changes in the mid- to late Holocene archaeological record in Australia have been interpreted as a reflecting a change in settlement pattern that included longer periods of

site occupation and exploitation of a wider array of resources and technology as compared to the Pleistocene. This "intensification" of resource exploitation and land use has been interpreted as being concomitant with the rise of more complex social structures, ceremonial activities, exchange and trade networks, and more permanent settlement patterns observable during European contact period (Lourandos 1980, 1983, 1985; Beaton 1990). Proponents of the "intensification theory" note that this change involved, but was not contingent upon, increases in population density during the Holocene. Lourandos (1997) and others (e.g., Smith 1996; Smith 2005; Ross 1985) argue that the changes in late Holocene resource use, particularly the inclusion of grass seeds into the diet of foragers living in the arid zone, are indicative of prehistoric Australians engaging in the "broad spectrum revolution" (Flannery 1969) observed in other societies as a prelude to the rise of agriculture.

The data presented here and elsewhere provide insight into burning and foraging behavior that can contribute to explaining this pattern of very recent diet broadening in the arid zone. Our data indicate that the growth of historically exploited grass seeds (such as *Eragrostis* spp.) is encouraged by anthropogenic burning. Why, then, did hunter-gatherers inhabiting the region for millennia only begin relying on the resource intensively in the last 1500 years? Recall that the proliferation of edible plant foods, including seed grasses, occurs as an *effect* of burning to acquire another resource that provides higher foraging returns. The archaeological signature of arid zone use throughout the Pleistocene and into the Holocene suggests it was created by highly mobile foragers living at low population densities. These foragers may have targeted the high foraging returns available from burning, perhaps hunting burrowed game in desert

regions on a seasonal basis without having to include lower ranked resources with high processing costs into their diets.

The contemporary spatial distribution of Martu anthropogenic fire scars in the Western Desert shows how the carefully controlled burning of coarsely grained habitats by Martu women during burrowed game hunts shapes the landscape into small patches distributed at spatial scales equivalent to a human foraging range (Bliege Bird et al. 2008b, 2012). This suggests that, if unrestricted by competition from other individuals on the landscape, Pleistocene arid zone foragers could have tracked the foraging opportunities associated with naturally occurring fires, and/or employed a "burn as you go" strategy, following the high return rates provided from landscape burning and hunting burrowed game.

The plausibility of this scenario, however, is contingent upon population densities, and therefore resource competition, remaining low in the arid zone for tens of thousands of years. Recent comparison of radio-carbon density time-series analysis and long-term records of climate change suggests that climatic fluctuations significantly impacted prehistoric Australian populations, keeping them low throughout the Pleistocene. Critics of using C14 counts as demographic proxies point out that taphonomic processes result in declines in site frequencies and datable materials over time, independent of changes in human population size (see Holdaway et al. 2008 for Australia; Surovell and Brantingham 2007 for North America). Therefore, the increase in archaeological materials observable worldwide during the mid- to late Holocene may be the result of differential preservation of newer materials rather than an indicator of demographic change. Recent work, however, argues that taphonomic effects are insufficient to

completely explain the increase in archaeological materials apparent during the latter part of the Holocene, suggesting a general increase in human population numbers is likely indicated (Johnson and Brook 2011; Surovell et al. 2009).

Smith et al. (2008:399) interpret observed changes in radiocarbon frequencies in the Australian archaeological record as reflecting population increases and crashes over time, and present a "first-order approximation of long-term prehistoric population trends in Australian drylands." This data set, which encompasses all regions within the arid zone (i.e., the arid coast, the Pilbara and Murchison regions, the arid central desert, and the Southeast arid zone and Murray-Darling river basin), shows the occurrence of six significant population events since 20 kya BP: The oldest, at 19 kya, is seen to reflect increased occupation densities in the Murray-Darling regions associated with the last remnants of glacial lakes in the Willandra region. The next inferred population peak from 16-14 kya appears to have occurred widely during the period following LGM, with the third being limited to the arid coast around 10.5 kya. Coastal areas appear to have higher population densities again at 8 kya, likely due to sea level transgression creating resource-rich mangrove swamps (Woodroffe et al 1985; Mulrennan and Woodroffe 1998), and higher populations are also associated with the major river systems that were experiencing increased discharge at the time. The fifth increase in population density occurred from 5 to 3 kya, and was most significant in the Murchison and Pilbara regions, but likely occurred in the arid interior as well. In most regions, populations appear to rebound rapidly after a collapse inferred at 3-2.5 kya BP, but recovery is not fully apparent archaeologically in the arid zone until 1.5 kya BP. Evidence indicates the most significant increase in regional population density from this

point in time until European contact.

This analysis generally suggests that climate amelioration during the Holocene allowed for rapid and significant demographic growth, with populations of arid zone hunter-gatherers moving into and inhabiting previously unoccupied or lightly populated areas. Evidence of sustained demographic growth in the arid zone does not appear until 8 kya BP, with the most significant period of population increase occurring around 1.5 kya (Smith et al. 2008), directly correlating with the emergence of seed processing technology in the archaeological record.

The data presented here on the short- and long-term foraging benefits produced by burning can contribute to an explanation for the recent intense reliance on resources with high processing costs. Using contemporary Martu burrowed game hunting as an analog, consistently higher foraging return rates would be achieved if it were possible to burn and hunt continuously. Sustaining this foraging strategy, however, requires a consistent source of fuel (in this case unburned spinifex). Given the minimum five-year period of regrowth needed for spinifex to sustain a fire, increased population density with increased burning must restrict options of moving to areas that can sustain a fire. As population density in a given area increases, the foraging landscape becomes burned out. Therefore, reliance on the plant foods that emerge in succession after a burning episode would become increasingly important for survival until even resources that require significant processing are included in the diet. We suggest that the unprecedented rapid population growth in the Australian arid zone during the late-Holocene restricted mobility and burning ability to the point that adopting a broader diet, and the processing technology it requires, became the only sustainable strategy.

1.7 Conclusion

The evolutionary significance of fire for human mobility and resource use cannot be overstated as the data presented here on the behavioral ecology of Martu burning practices illustrates. Much has been written about the role of Aboriginal burning practices as a plausible mechanism for ecosystem reorganization and subsequent megafaunal extinction after initial human colonization of Pleistocene Australia (see Mooney et al. 2011 for recent review). Observations of fire use among Australian Aborigines have been extrapolated into the past and subsequently implicated as the cause of vegetation changes observable in charcoal and pollen records (e.g., Kershaw 1986; Singh et al. 1981; Wang et al. 2005), and in the disappearance of large bodied mammals during the Pleistocene (e.g. Miller et al. 2005). Our data show that proactive landscape modification in the Australian arid zone achieved through burning presents beneficial foraging opportunities as well as costs, and is constrained by the time required for vegetational regrowth to provide sufficient fuel to sustain burning. We suggest that arid zone Aboriginal burning practices observed after European contact and the fine-grained vegetational mosaics they create are a mid- to late Holocene phenomenon shaped by population density, reduced mobility, and climatic stabilization. It follows, then, that extending these practices into the deeper past by analogy to explain large-scale environmental change and/or megafaunal extinction is likely inappropriate, especially given evidence of lower human population densities and a greater degree of climate flux in Sahul during the Pleistocene. We hope that the analysis presented here encourages more exploration into the various ways humans use fire in different

ecological settings, and stimulates further discussion of the importance of fire use in human evolutionary history.

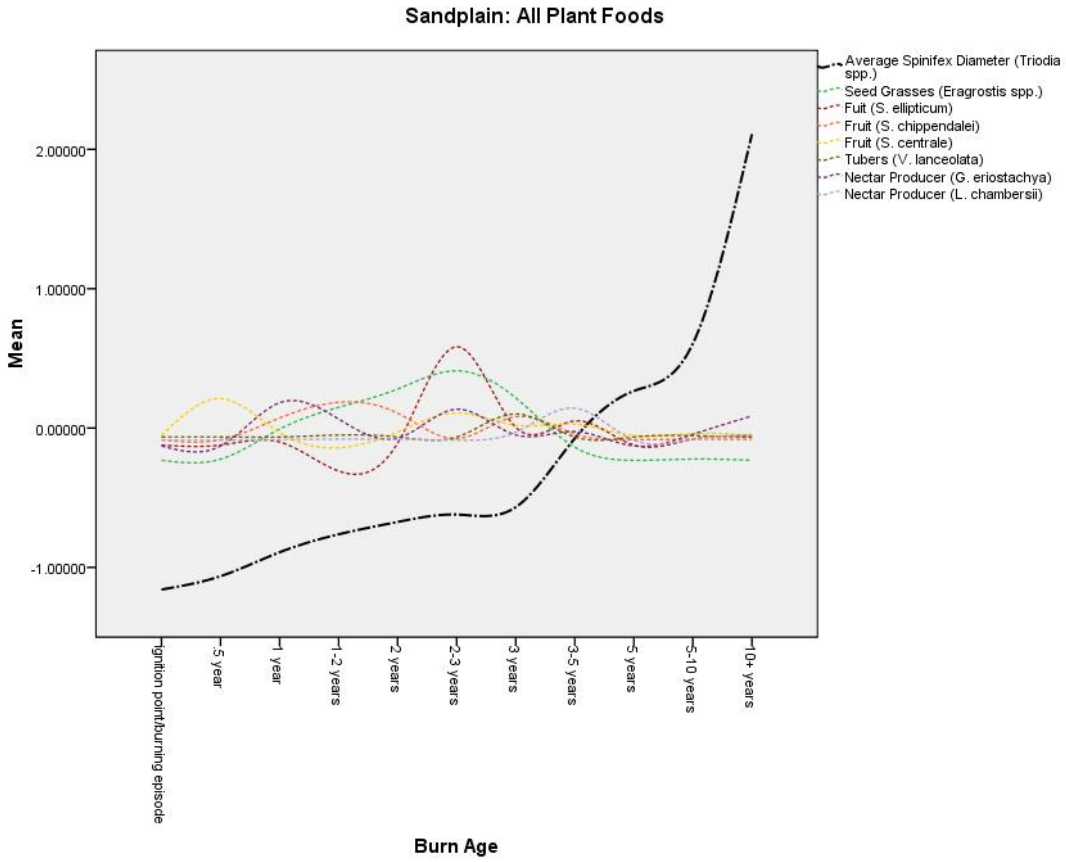

Figure 1.1: The postignition regrowth pattern of spinifex and selected plant foods, including seed grasses, fruits, tubers, and nectar producers in the Sandplain ecozone. Stem counts for each plant food recorded during transects and average spinifex diameter measured in systematically placed quadrats are assigned z-scores for normalized comparison on the Y axis. The X axis shows temporal intervals of regrowth. Growth peaks for fruit are observable at roughly six months (*S. centrale*), between one to two years (*S. chippendalei*), and two and a half (2.5) years (*S. ellipticum*), respectively. All fruit-producing plants reach their highest population density within three years of regrowth after a burning episode. Seed grasses (*Eragrostis* spp.), tubers (*V. lanceolata*), and one species of nectar producer (*G. eriostachya*) reach peak density after two to three years of regrowth, with nectar-producing *L. chamberseii* populations peaking three to five years after a burn. The population densities of all food plants decline after five years of regrowth, at which point average spinifex diameter has increased to the point of dominating groundcover.

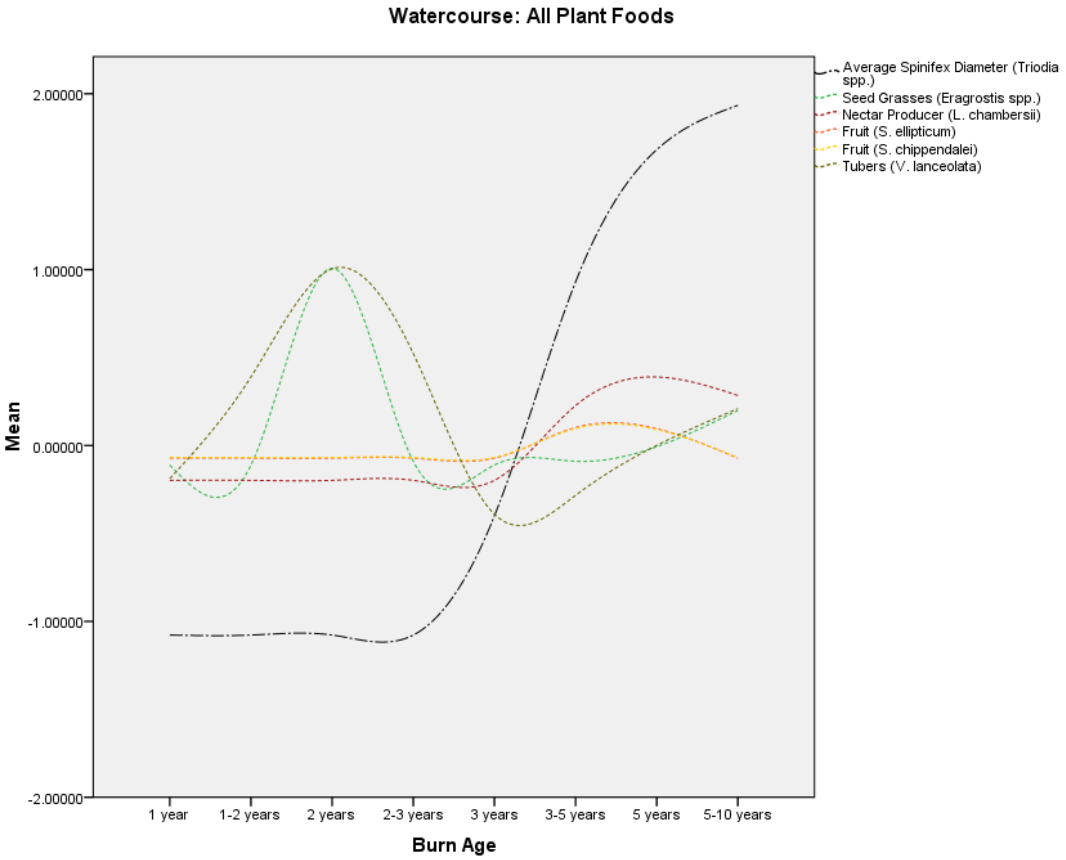

Figure 1.2: Regrowth pattern of plant foods in the watercourse ecozone. Seed grasses and tubers reach peak density around two years after a burn, with populations of tubers declining at a slightly slower rate than seed grasses. By three years after a burning episode, spinifex has reached sufficient density to dominate groundcover in the ecozone.

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CHAPTER 2

THE PYROPHILIC PRIMATE HYPOTHESIS

2.1 Abstract

Members of genus *Homo* are the only primates known to create and control fire. The adaptive significance of this unique behavior is broadly recognized, but the steps by which our ancestors evolved pyrotechnic abilities remain unknown. Many hypotheses attempting to answer this question attribute hominin fire to serendipitous, even accidental, discovery. Using recent paleoenvironmental reconstructions, we present an alternative scenario that instead suggests that human fire dependence is the result of adapting to progressively fire-prone environments during the Plio-Pleistocene transition. The extreme and rapid fluctuations between closed canopy forests, woodland, and grasslands that occurred in tropical Africa during that time, in conjunction with reductions in atmospheric carbon dioxide levels, changed the fire regime of the region, increasing the occurrence of natural fires. We use models from Optimal Foraging Theory to hypothesize benefits that this fire-altered landscape provided to ancestral hominins and link these benefits to steps that transformed our ancestors into a genus of active pyrophiles whose dependence on fire for survival contributed to its rapid expansion out of Africa.

2.2 Introduction

Within the primate order, the ability to habitually create and control fire is unique to members of genus *Homo*. The adaptive significance of anthropogenic fire use is broadly recognized, and Darwin noted its evolutionary importance in *the Descent of Man*, deeming it "…probably the greatest [discovery], excepting language, ever made by man" (Darwin 1871 [1981]:137). Efforts to determine when this "greatest discovery" occurred and fire use became an inextricable part of hominin behavior remain inconclusive and controversial. The earliest strongly suggestive archaeological evidence of controlled fire use by hominins comes from intact sediments dating to 1 million years ago from Wonderwerk Cave, South Africa (Berna et al. 2012). Other African archaeological sites such as Koobi Fora FxJj20 East (Bellomo 1994; Rowlett 2000), Chesowanja GnJi1/6E (Gowlett et al. 1981, 1999), and Swartkrans (Brain 1993; Sillen and Hoering 1993) indicate possible use of fire by genus Homo at 1.5 Ma, 1.42 $\pm$ 0.7 Ma, and 1.0-1.5 Ma, respectively. Despite archaeological indications dating to 1 million years ago and older, many researchers posit that strong evidence of habitual controlled fire use does not appear in the archaeological record until the Middle Paleolithic ~400 kya (e.g., Roebroeks and Villa 2011a,b) or even as late as the Upper Paleolithic (Sandgathe et al. 2011a,b).

Other lines of evidence suggest an even greater antiquity of fire use for our genus than indicated by the earliest archaeological signatures. Anatomical changes appearing in hominid fossils dating to the Early Pleistocene, such as smaller teeth and reduced masticatory architecture relative to extant nonhuman primates and Australopithecines, are argued to reflect physiological adaptations to consuming cooked foods (Burton

2011; Carmody and Wrangham 2009; Wrangham 2009; Wrangham and Carmody 2010). Wrangham's "cooking hypothesis" suggests a compelling association between an adaptation to eating cooked food and the distinctive morphological changes seen in the well-defined hominid fossil form *H. erectus* (also *H. ergaster*, or Early African *H. erectus,* Wood 1992), which dates to roughly 1.8 Ma in Africa (Feibel et al., 1989; White, 1995). This evidence is often disregarded due to its mismatch with an archaeologically based timeline of human fire use arising in the Middle Paleolithic. Wrangham (2007:313) defines the discrepancy between the anatomical evidence of a reliance on cooked foods in *H. erectus* and archaeological evidence of fire use as the "cooking enigma": "On the one hand, cooking is absent among animals, universal in humans, and rich in biological consequences. It is therefore expected to have a strong impact on evolutionary biology. On the other hand, archaeological data place the acquisition of cooking at a time when nothing dramatic was happening in human evolution."

While debate about when fire use is archaeologically indicated for our genus continues (Gowlett and Wrangham 2013; Roebroeks and Villa 2011a,b; Sandgathe et al. a,b), the core of the "cooking enigma" reflects a more fundamental gap in our knowledge of hominid fire use—how did hominins come to use, control, and create fire? The inception of this distinctive behavior, and its incorporation into the behavioral repertoire of our genus, are often hypothesized to be the result of happenstance or accidental discovery. Wrangham (2009:191-192) constructs one such evolutionary scenario of fire discovery wherein,

> during the tens of thousands of generations between the origin of habilines (at least 2.3 million years ago) and *Homo erectus* (at least 1.8 million years ago), from time

> to time the sparks resulting from habilines' pounding rocks could have accidentally produced small fires in adjacent brush. Perhaps cocky juvenile habilines dared to grab the cool end of a branch and tease one another with the smoldering twigs or blazing leaves, much as young chimpanzees playfully bully one another with sticks they use as clubs. Adults learned the effect on one another of waving a burning log. The practice of scaring others with fire was then transferred to the serious job of frightening lions, sabertooths and hyenas, similar to how chimpanzees use clubs against leopards. At first the fires went out. But over time, when sparks happened to start a fire, habilines learned that it was worth their while to keep it going. They cultivated fire as a way to help them defend against dangerous animals.

This scenario in many ways echoes Darwin's favored hypothesis for the advent of human fire use proposed by John Lubbock (1865) in which the discovery of fire was the result of lithic tool manufacture. The commonality in both of these scenarios, and others like them, is that initial benefits of fire were serendipitous byproducts of another activity (e.g., simple stone tool construction). Once the benefits of this accidental discovery were recognized, fire use was adopted as a technological innovation for myriad purposes, including light, warmth, predator defense, and cooking. Gowlett (2010:342) highlights one reason why "accidental discovery" hypotheses often approach the advent of fire use as an "add on" to technology in our genus' evolution: "[Fire's] presence is harder to document than that of stone tools, so the general assumption is that it appears later."

Here we follow others in acknowledging the necessity of regular exposure to natural fire for pyrotechnic ability to evolve (e.g., Gowlett 2010; Gowlett and Wrangham 2013; see also Wrangham 2009:192-193), but offer an alternative scenario that does not rely on accidental discovery. We propose instead that our genus' distinct pyrophilia is the result of adapting to an increasingly fire-prone Early Pleistocene environment by exploiting the foraging benefits provided by naturally occurring fires. These benefits included improved efficiency in travel, resource detection and acquisition, and a

reduction of processing costs. Fire control in the form of simple landscape burning and purposeful cooking followed as a consequence of targeting the innovative foraging benefits of fire. We construct our scenario by briefly reviewing recent environmental and climatic reconstructions of tropical Africa during the Plio-Pleistocene transition to establish the ecological context in which an increase in natural fires introduced new selective pressures for hominins. We then use modeling tools from Optimal Foraging Theory to identify novel foraging benefits created by this fire-altered environment. We conclude by discussing the ecological and behavioral consequences for ancestral humans. Our scenario provides a 'basal solution' to the cooking enigma identified by Wrangham (2007:314), in that it suggests "that cooking was adopted around the origin of *Homo erectus* and was responsible for many of the features that characterize human evolutionary changes from australopithecines." We argue, however, that cooking is one component of a specialized adaptation *to fire itself*, with *Homo* being an actively pyrophillic primate wholly dependent upon fire for its survival and reproduction.

2.3 Materials and Methods

Environmental change has long been nominated as a selective force in human evolution, especially with regard to changes from wooded to more open "savannah" environments. The last common ancestor we share with chimpanzees is widely recognized as inhabiting wooded environments, which became increasingly more open after 5-8 million years ago, roughly contemporaneous with our divergence from that common ancestor (Wood and Harrison 2011). The increased prevalence of savannah ecosystems has been suggested as having influenced hominin dietary and locomotor adaptations (e.g., Rogers et al. 1994; Sept 1998; Wheeler 1994; Richmond et al. 2001;

Teaford and Ungar 2000), but debate over the timing and degree to which this "savannah hypothesis" explains hominin evolutionary change has continued since it was first formulated by Dart in 1925 (see Domínguez-Rodrigo 2014 for review).

Recent paleoenvironmental reconstructions derived from stable carbon isotopes in palaeosols (Segalen et al. 2007; Cerling et al. 2011a,b) have clarified the dating and extent of grassland expansion in tropical Africa since the Late Miocene (~7 million years ago). Stable isotopes are particularly useful in paleoenvironmental reconstructions because woody plants use the C_3 photosynthetic pathway, while tropical grasses use the C_4 pathway. These two pathways discriminate against $^{13}CO_2$ differently during photosynthesis, allowing for the carbon isotopic composition of soils to be used as a direct indicator of the fraction of woody cover versus more open grasslands in tropical environments (Pearcy and Ehleringer 1984; Wynn and Bird 2008; Lloyd et al. 2008; Cerling et al. 2010). Recent analysis of $^{13}C/^{12}C$ ratios in palosols from the Awash Valley and the Omo-Turkana basin spanning the time period from 7.4 million years ago (Myr) to the present indicate a pattern of relatively open conditions in the Late Miocene to Early Pliocene, followed by a general increase in woody cover in the Middle Pliocene (~3.6 Myr ago). The Plio-Pleistocene transition (~3.6-1.4 Myr ago) indicates a return to more open environments, with the extent of open grasslands peaking at roughly 1.8 Myr ago (Cerling et al. 2011b). Extending the approach of Cerling et al. (2011b) by including lipid biomarkers preserved in ancient lake sediments at Olduvai Gorge, Magill et al. (2013) provide a more precise picture of ecosystem fluctuation between forests, woodlands, and open grasslands between 2.0 and 1.8 Myr ago. Using definitions of African plant communities established by UNESCO for clarity (e.g.,

grassland, wooded grassland, woodland, and forest), their analysis shows four fluctuations to open grasslands from wooded grassland, woodland, and closed canopy forests in the span of 100,000 years at Olduvai.

This pattern of extreme, rapid ecosystem change from landscapes dominated by C_3 plants to more open C_4 plant communities appears driven by reductions in atmospheric CO_2 levels and acute increases in aridity. The combination of these factors also likely changed the fire regime for large parts of tropical Africa, with a higher prevalence of natural fires occurring given the drier conditions and more combustible fuel sources in the form of expanding grasslands and wooded grasslands. Africa is often referred to as "the fire continent" (Komarek 1971) due to widespread burning throughout its sub-Saharan grasslands, which stabilized at more or less their current extent after 1.8 Myr ago. The mixed vegetation communities that appeared with each fluctuation in grass (C_4) versus woodland/forest (C_3) dominated landscapes also presented novel foraging challenges for primates adapted to extracting nutrients from more wooded environments. Due to the frequency of burning in sub-Saharan Africa, many plants and animals living there have adapted to cope with–and even benefit from–fire (Goldammer and De Ronde 2004; Lyon et al. 1978), and we suggest that the bipedal primates inhabiting tropical Africa during the Plio-Pleistocene transition did as well.

2.4 Theory

Hominins, like all organisms, are products of an evolutionary history shaped by natural selection with all the characteristics of adaptive design (Williams 1966). Assumptions about adaptation profitably guide investigations of behavioral variability across time and space specifically as it relates to subsistence (Ydenberg et al. 2007).

Behavioral ecology studies the fitness-related trade-offs organisms face in specific ecological settings. The set of foraging-related models developed in this research tradition, *optimal foraging theory,* focuses on the economics of nutrient acquisition and the decisions foragers make on the food quest (Stephens 2008; Stephens and Krebs 1986). Optimal foraging models assume a goal or fitness-related outcome, trade-offs, currency, and an opportunity set for foragers. Because of its generalized nature, objective approach to decision-making, and economic orientation, the applicability of the prey model to humans became quickly apparent (Smith 1983).

2.4.1 The Prey (or Optimal Diet) Model

This is the most widely used foraging model from behavioral ecology (Emlen 1966; MacArthur and Pianka 1966). It simplifies foraging activities into two, mutually exclusive components, searching and handling. The model assumes a forager's goal is to maximize its net rate of nutrient gain, and poses the foraging decision as a single, repetitive, yes/no choice each time a possible food resource is encountered. The answer will be no if the forager can expect to do better by continuing to search for something better. The *currency* used to measure the value of the choices is typically the expected rate of energy acquisition (kcal/hr) they represent. Resources are ranked by their expected net profit of energy per unit of time spent in handling (their return rate once found, so exclusive of search time). Highest ranked resources are always taken on encounter with lower-ranked resources taken or not depending on whether their profitability is higher than the expected rate for continuing to search, which depends on the expected encounter rates with higher ranked resources.

2.4.2 The Patch Choice Model

The Patch Choice model (MacArthur and Pianka 1966), identifies the tradeoff between earned returns within a patch and travel time between patches in an environment where resources are clumped instead of randomly distributed. The forager's goal is to maximize the net rate of return per unit foraging time by exploiting the optimal array of patches. Decision variables in the patch model are enter a patch or bypass it to travel to (search for) another with a higher rate. The patch model treats patches as the optimal diet model treats individual prey items.

2.4.3 Improvements in Foraging Efficiency/Foraging Innovations

Predictions generated from optimal foraging models continue to help researchers explain foraging variability within and across taxa (Krebs and Davies 2009; Pyke et al. 1977; Stephens 2008). The elegant link between diet breadth and time allocated to either search or handling has important implications for understanding changes in subsistence-related behavior (Hawkes and O'Connell 1992). Broader diets include less profitable resources and so require that more time be devoted to *handling*; under these conditions, innovations that improve handling efficiency will have their greatest effect. A model forager maximizing their overall rate of nutrient gain per unit time should adopt such innovations where diets are already broad, because that is the *only* way to achieve higher food acquisition rates in such situations. Conversely, when diets are narrow, more time is devoted to search. As a consequence, improvements in search efficiency should be favored to increase encounter rates with profitable food types. Controlled fire use is such a foraging innovation. It is unique in that it increases foraging efficiency by reducing the amount of time required to both search for and

process food resources in two ways: cooking and landscape burning.

2.4.3.1 Cooking as handling reduction

Wrangham (2009; 2010) argues that the primary human benefit from fire lies in the dietary advantages of cooked foods, and that the physiological adaptations to this benefit are apparent in the morphology of *Homo erectus* 1.8 million years ago. Cooking (i.e., chemically altering a resource through the application of fire) can be viewed as a handling improvement because reductions in chewing effort (Dominy et al. 2008), and chemical alterations that increase digestive efficiency (Carmody and Wrangham 2009; Oka et al. 2003) lower handling (processing) costs. For example, fire treatment improves protein digestibility in seeds and nuts (Kataria et al. 1989), the digestibility of underground storage organs by neutralizing toxicity (Carmody and Wrangham 2009) and gelatinizing starchy tissues (Wansnider 1997). Cooking also increases the fracture rate for some tubers by 49% (Dominy et al. 2008). Cooked meat is easier to chew and digest because tough tissues have been denatured (Waldron and Smith 2003). All of these alterations make the nutrients in these resources more readily available and accessible, reducing handling efforts that raise resource profitability and ultimately result in higher return rates.

Cooking improves handling efficiency so effectively that it changes the prey type of some resources. Recall that the optimal diet model ranks resources by their expected net profit of energy per unit of time spent in handling. If this rate increases, i.e., more nutrients can be extracted and used more efficiently, the profitability of that resource increases, and its ranking improves. When cooking increases the bioavailability of nutrients that can be extracted from a resource via chemical and/or mechanical

alteration, the handling cost of that resource is reduced. A cooked tuber, for example, will be a different prey type within the framework of the optimal diet model than an uncooked tuber, despite taxonomically being the "same" resource; cooking changes the profitability of the tuber by raising the nutrients extracted over the time spent processing it. Cooking changes the profitability of some resources so significantly, it is the only way they can be consumed. The North American tuber Camas (Camassia quamash), which requires extensive cook-times to become edible, exemplifies the power of cooking as a handling innovation (Thoms 1989).

2.4.3.2 Landscape burning as search reduction

Cooking improves handling efficiency by increasing the bioavailability of food energy, but fire can also act to reduce search costs inherent in food collection. There is considerable evidence that low-cost, large-scale habitat burning is commonly used by modern human foragers with relatively broad diets to reduce the amount of time required for search during foraging by increasing encounter rates with economically important resources (Keely 1995). Data from Australia show that anthropogenic burning practices employed in the Western Desert are driven and sustained by the immediate foraging benefits acquired by Martu Aboriginal women during seasonal burrowed game hunts (Bliege Bird et al. 2008; Bliege Bird and Bird 2008; Bird et al. 2005). Burning off ground cover immediately increases search efficiency for Martu women by exposing the holes and tracks of target species that are otherwise obscured. This increased visibility improves hunters' ability to read and interpret the subtle clues indicating whether a den is occupied and therefore likely to be productive. Burning allows hunters to more efficiently and predictably encounter, pursue, and process

burrowed prey by reducing the amount of time allocated to search and handling activities. Landscape burning is a resource manipulation technique used by many traditional peoples that serves several broad functions, including clearing low plant cover, altering the composition of resources in a given area by opening up land for faster growing fire adapted foliage, and changing the distribution of animal species over a particular area (Allan and Southgate 2002; Jones 1969; Kimber 1983; Masipiqueña et al. 2000; Pyne 1995; Tothill 1971). Each of these functions ultimately serves to decrease time spent searching for and traveling to food items, thereby reducing search and travel costs.

2.5 An Evolutionary Scenario

Paleoclimatic reconstructions of Olduvai Gorge 1.9 to 1.8 mya indicate rapid, recurring ecosystem fluctuation between closed C3 woodlands and open C4 grasslands within the context of a generalized long-term climatic trend toward cooler and drier conditions. Imagine a bipedal ape already adapted to consuming resources isotopically consistent with mixed savanna/woodland environments (Cerling et al. 2011b; de Ruiter et al. 2008; Lee Thorpe et al. 1994; Sponheimer et al. 2007) with life history characteristics assumed to be similar to those of the modern chimpanzee inhabiting this rapidly changing environment. Each expansion of grassland and reduction of forests would have presented a foraging dilemma; foods in forests would be increasingly unavailable as grasslands expanded, necessitating a foraging adaptation to this novel environment.

2.5.1 Pyrogenic Improvements in Search and the Capture of Fire

We suggest that the immediate ancestor of *Homo ergaster/erectus* adapted to aridity-driven ecosystem change and grassland expansion by taking advantage of the innovative foraging effects fire provided in grassland habitats. While other primates contemporary with the predecessor of *H. erectus* such as *P.bosei* and *Theropithecus* adapted to savanna ecosystems by specializing in grass and/or sedge consumption (Cerling et al. 2011a), this environment provided fewer foraging opportunities compared to woodlands and forests for other primates. Naturally occurring grassland fires are a common feature of the dry season in many temperate biomes (Seydack et al. 2007; Van Wilgen et al. 2004), and while these fires negatively impact grazing animals by eliminating their forage for a time, they improve foraging opportunities for nongrazers in grass-dominated landscapes by removing ground cover that otherwise obscures many available resources. Gowlett (2010:349) notes how "[fire] exposes roots, tubers, small animals and their burrows, birds' nests and eggs, sometimes ready cooked…" (2010:348-349). Fire in grassland environments uniquely alters the landscape by creating a resource patch with reduced search and travel costs.

These patches would have been particularly attractive to hominins during acute dry seasons when the resources from already contracting forests and woodlands, such as fruits and nuts, were unavailable. Resources remaining on the ground surface after a fire, such as insects, larvae, reptiles, small burrowing animals, seeds, and shallow-rooting tubers, provided new foraging opportunities especially appealing to a bipedal ape given the fire-induced removal of obstacles to locomotion and prey detection. Smoke and circling avian species similarly attracted to the immediate foraging opportunities created by fire (Goldammer and De Ronde 2004; Meester et al. 1979;

Ream 1981; Bouwman and Hoffman 2007) signaled the creation of these pyrogenic resource patches, and savanna dwelling hominins increasingly reliant upon foods available from them surely associated these signals with food acquisition.

Repeated exposure to seasonally occurring natural fires and the resource patches created by them would link landscape burns to increased food availability for the predecessor of *H.ergaster/erectus*. The temporally and spatially predictable resource patches created by natural fires converted grass-dominated landscapes with few foraging opportunities into relatively rich resource patches in which food items are encountered at a higher rate. Burning had a positive rather than negative impact on grassland foraging opportunities by transforming lower ranked patches into higher ranked patches with more profitable resources and lower search and travel costs. Repeatedly encountering this link between burns and increased foraging returns, behaviorally flexible hominins could have extended their gains by moving still-burning or smoldering wood and/or grasses from burned patches across naturally occurring fire breaks. By spreading fire to unburned patches and expanding the burns, they could increase their opportunities to earn the higher foraging return rates that follow fires.

The act of simply transporting fire from burned to unburned areas and firing them would have provided several adaptive advantages in food acquisition for Pleistocene hominins. They were likely not the only animals that recognized and took advantage of the foraging benefits available in fire-created resource patches. Birds indicating the presence of fire from afar also act as immediate competitors for the resources exposed on the surface of burned patches given their ability to fly over instead of walking through unburned stretches of grass. Preserving fire for a short time, moving it to an

unburned area, and applying it to the landscape allowed hominins to reduce any competitive advantage avian species, among others, would have in burned-patch exploitation. Controlling the creation of higher-ranked patches ensured they were the *immediate* recipients of the available foraging benefits. Minimally controlled burning modified the landscape in a way favorable to their foraging goals, creating a predictable foraging niche. Such simple fire-controlling behavior, arising from frequent exposure to naturally occurring fire and the identification of its positive effects on foraging, need not involve anthropogenic fire creation, or even long-term fire maintenance to provide an adaptive advantage. Even if it was initially maintained on a purely seasonal basis (i.e., during dry seasons), the adaptive advantages it provided likely increased positive selective pressure on its inclusion into our behavioral repertoire.

2.5.2 The Importance of Geophytes and Pyrogenic Improvements in Handling (Purposeful Cooking)

Wrangham (2009; 2010) argues that the primary human benefit from fire lies in the dietary advantages of cooked foods and the physiological effects of adapting to reap this benefit are apparent in the morphology of *Homo erectus* 1.8 million years ago. Gowlett (2010:348-349) notes that one of the foraging benefits of natural grassland fire is that it "ready cooks" many of the resources available in the patch it creates as it moves through the landscape. As we note above, cooking is a foraging innovation that improves the rate of energy acquisition by altering the properties of food in a manner that increases the efficiency of nutrient extraction. In many ways, the effect of fire treatment on individual resources mirrors its effect on grass-dominated landscapes by improving their foraging utility. This alteration is so powerful in some cases that it

renders otherwise toxic, inedible resources edible and nutritious. Given the benefits of cooking, it might emerge in the context of repeated exposure to naturally occurring fires, or as an augmentation of simple fire controlling/preserving behavior.

Purposeful cooking, however, does not necessarily follow from evolutionary scenarios involving adaptation to fire-prone environments. If one of the foraging benefits associated with naturally occurring fires is that they create patches where food items can be more easily located and captured, many of which are "ready cooked" as a consequence, what would lead to purposeful, directed anthropogenic fire use for intentional cooking? If food is already cooked via a natural, frequently occurring phenomenon, there would be no pressure for purposeful cooking. Therefore, purposeful cooking is not a necessary component of the evolutionary scenario we have so far constructed here in which the simple fire controlling behavior of capturing and transporting fire to favorably adjust the foraging landscape also creates patches with ready-cooked foods. While this might be loosely categorized as "purposeful cooking," it is more accurately described as a beneficial consequence of landscape modification—"unintentional" rather than "intentional" cooking.

The selection for intentional cooking behavior more likely arose to beneficially alter foods via fire treatment that would otherwise be unaffected by landscape firing, i.e, foods isolated from the effect of flame and heat. The underground storage organs of some plants (hereafter, "geophytes"), most commonly found in seasonally dry habitats among the *Liliaceae, Dioscoreaceae, Araceae, Taccaceae*, and *Icacinaceae* families, meet this criterion (Raunkiaer 1934; Thoms 1989). Geophytes are often nominated as an important component of early hominid diets (Hately & Kappelman 1980; Isaac 1980;

McGrew 1992; O'Connell et al. 1999; O'Connell et al. 2002; Peters and O'Brien 1981; Stahl 1984; Vincent 1985; Wrangham et al. 1999). Sequestering water and carbohydrates in underground storage organs is an evolved response of plants to adapt to habitats that undergo periods of seasonal aridity or cold (Thoms 1989), making them an attractive food source for foragers who can effectively process them, particularly during periods of seasonal aridity. Geophytes are also an attractive resource because they are "(1) generally available, especially in the dry season, (2) capable of yielding returns high enough to support the collector and at least one other person, [and] (3) reliable enough to provide those returns with little or no daily variance…" (O'Connell et al. 1999:470).

All geophytes, however, are not the same. They vary in form (i.e., bulbs, corms, rhizomes, taproots, tubers, and woody root stocks), and in degree of chemical and mechanical defense (Anderson 1987; Coursey 1973; Thoms 1989), which results in different handling costs, and therefore prey type. For example, geophytes with low levels of mechanical defense, such as the shallow rooting *makalita* (*Eminia antenuliffera*), are easily harvested by Hadza children, whereas consuming the deeply-rooted *//ekwa* (*Vigna frutescens*) "requires both substantial upper body strength and endurance to collect ***and the ability to make and control fire to process***" (O'Connell et al. 1999:466 [emphasis added]). In the scenario of pyrogenic patch creation presented here, consumption of deeply rooted geophytes similar to *//ekwa* would necessitate purposeful cooking, whereas shallow-rooting geophytes like *makalita* would likely have been subject to the passive cooking effects of landscape burning. Shallow rooted geophytes, while accessible to juvenile human foragers, are also available to other

animals: “The Hadza experience intense competition with savanna baboons (*Papio anubis*) for many of the same foods including all the berries, baobab, some small game, some honey, and even some shallow tubers. It is fortunate for the Hadza then that the baboons cannot take the deep tubers that Hadza women get.” (Marlowe and Berbesque 2009:756). Other nonhuman primates have also been observed exploiting shallow-rooting geophytes, including chimpanzees (Hernandez-Aguilar et al. 2007).

While fewer animals compete directly with humans by targeting and consuming deeply-rooting geophytes, those that do likely provided one avenue through which they became a viably exploited food resource for our ancestors. Fossil evidence indicates suids, which also rely on geophytes as a food source, increased in taxonomic diversity roughly contemporaneously with dates for early African *H. erectus* 1.8 million years ago (White 1995). The carbon isotope ratios of modern African warthogs (*Phacochoerus africanus*) overlap with those of *H. ergaster* and some Australopithecines and has been interpreted as evidence of overlapping diets, including geophyte consumption (Marlowe and Berbesque 2009:756-757; Yeakel et al. 2007). Elephants (*Loxodonta africanus*) and naked mole rats (Yaekel et al. 2007) also exploit deep-rooting geophytes, but elephants and warthogs (and suids generally) dig to extract tubers, whereas naked mole rats burrow to consume them below the ground surface. Any unconsumed geophytes brought to the surface of the ground in the course of digging by suids or elephants would be subject to the passive cooking effects of anthropogenic and naturally occurring landscape fires.

Geophytes excavated by other species to ground surface, then left to a landscape fire that cooked them, would have been an attractive resource for hominins. Within the

framework of The Diet Breadth Model, they would be a *higher ranked prey type* than the raw, subterranean uncooked plant part which has higher extraction and processing costs. The improved profitability of fire-altered deep rooting geophytes, which are otherwise isolated from the positive effects of landscape burning, would rapidly become apparent. Such direct evidence that exposure to fire raises the profitability of these foods could have driven selection for purposeful cooking. As hominins pursued the more profitable "cooked geophyte" prey type, reliance on the surface leavings of other species could have been circumvented by minimal investment in simple extractive technology such as digging sticks, increasing encounter rates and the proportion of these foods in the diet.

2.6 Discussion

The evolutionary scenario presented here suggests that human fire control and use was driven by a focus on the foraging benefits provided by naturally occurring fires during periods of aridity-driven grassland expansion ca. 2 million years ago. These benefits included improved search efficiency for high ranked food items as well as increased energetic profitability of food items cooked by natural fires. The selective incentive to consistently and sustainably acquire these benefits drove the adoption of fire control in the form of simple short-term preservation and transport to unburned areas to predictably create patches from which nutrients could be acquired at a higher rate. Purposeful cooking evolved as a means to achieve the higher return rates for deep-rooting geophytes otherwise unaffected by natural or anthropogenic landscape firing, improving the profitability of this generally available, reliably acquired, high yield resource to such a degree that it became an important staple food source for human

populations throughout our evolutionary history.

We contend that consistent habitual fire use was adopted by the evolutionary predecessor of *H. erectus/ergaster* because it functions as a broad spectrum foraging innovation that improves both search and handling efficiency in the food quest. An improved ability to procure food energy is argued to have expanded the energy budget in *Homo,* increasing body mass and travel distance (Ponzer 2012). Reaping the unique benefits produced by fire fundamentally changed the energetic acquisition rates for early *Homo*, resulting in a distinctive adaptation to fire which set members of our genus apart from *Australopithecines* and grass or sedge consuming *Paranthropines*. This adaptive shift appears to be reflected in physiological adaptations such as reduced masticatory apparatus and tooth size (Burton 2009; Carmody and Wrangham 2009; Wrangham 2009; Wrangham and Carmody 2010). The marked reduction of molar size in *Homo erectus* cannot be accounted for simply by rates of craniodental and body size evolution in our lineage, suggesting that an abrupt change in diet at or near the emergence of the species at 1.9 Mya drove selection for smaller molars (Organ et al. 2011).

According to our evolutionary scenario, the coincidence of these morphological and physiological changes are the consequence of *H. erectus'* evolutionary predecessors specializing in taking advantage of the foraging benefits provided by fire, becoming the only primate specifically adapted to and dependent upon it for survival. The significance of this shift in human evolution may be described by employing the dichotomous nomenclature from botany characterizing variability in *pyrophytes*, or fire-adapted plants: *passive pyrophytes* resist the effects of fire and are therefore able to

outcompete less resistant plants in fire-prone environments; *active pyrophytes*, such as the *eucalypts* of Australia, enjoy a similar competitive advantage but also encourage the spread of fires beneficial to them by producing volatile oils (Grove and Rackham 2001;Trabaud 2000; Tishkov 2004). We suggest that genus *Homo* evolved as an *actively pyrophilic* primate that could not survive without exploiting the foraging benefits of fire, using it to shape its environment and expand out of Africa into Europe and Asia. This degree of pyrophilia could only be the result of selection within an environment regularly exposed to and altered by burning. The effect of this specialization resulted in *H. erectus* adapting as an *obligate pyrophile* dependent upon fire for survival and reproduction, an hypothesis supported by recent evidence indicating that the mass of neurons for an *erectus*-sized ape can only be metabolically supported by a cooked diet given the chewing times recorded for other great apes (Fonseca-Azevedo and Herculano-Houzel 2012).

As a component of our genus' pyrophilia, the importance of intentional cooking in our evolution cannot be overstated. Wrangham has reported extensively on the positive benefits of cooking (1999; 2001; 2003; 2007; 2009; 2010), and its impact on human evolution. Cooking food has fundamentally changed the food quest for humans in two specific and powerful ways. First, because cooking improves the profitability of foods by rendering them easier to chew and digest (i.e., reducing handling effort), human foragers target *higher ranked prey types* than our close primate relatives by default. More simply, the goal of a human forager searching coastal areas for shellfish, for example, is not the acquisition of the shellfish per se, but instead the higher-ranked *cooked* shellfish. Cooking food inexorably changed the foraging calculus for our genus,

and allowed for a greater range of foods to be exploited from environments otherwise unattractive to nonpyrophilic primates.

Second, cooking changes the way foods are collected and consumed. Humans, for the most part, are not immediate resource consumers like other primates. Instead, food is accumulated prior to processing for the simple reason that it is more efficient to cook en mass rather one item at a time (see Wrangham 2009:129-133). Leonetti and Chabot-Hanowell (2011) have explored the importance of women's roles in food processing and its effect on kinship and food distribution. The model we propose of intentional cooking evolving through the exploitation of deep-rooting tubers further illustrates the impact food accumulation would have on the social organization of *Homo*. Ethnographic data from Hadza hunter-gatherers show that, in contrast to shallow-rooting tubers, deep-rooting tubers are an inaccessible resource for human juveniles. The acquisition and accumulation of these tubers for the purpose of cooking, however, allows children to access nutrients otherwise unavailable to them. This provides a means by which the unique human characteristic of cooperative child rearing likely evolved, and would have been an especially attractive way for females with declining fertility to redirect resources to their children and grandchildren with profound evolutionary effects (Hawkes 2003, 2004, 2006, 2013; Hawkes and Blurton Jones 2005; Hawkes and Coxworth 2013; Hawkes, O'Connell, and Blurton Jones 1989, 1997; Hawkes, O'Connell, Blurton Jones, Alvarez, and Charnov 1998; see Kim, Coxworth, and Hawkes 2012 for formal modeling; O'Connell, Hawkes and Blurton Jones 1999).

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CHAPTER 3

ON THE ARCHAEOLOGICAL SIGNATURE OF HUMAN FIRE USE: ANALYSES, INTERPRETATIONS, AND IMPLICATIONS FOR UNDERSTANDING THE EVOLUTION OF PYROTECHNIC BEHAVIORS

3.1 Abstract

The importance of controlled fire use in human evolutionary history is widely acknowledged, but the timing of initial anthropogenic fire use and control remains contentious. This debate has recently extended to question whether fire-making behavior was maintained and employed by early hominins moving into northern latitudes. Using evidence from the European archaeological record, a series of recent publications contend habitual fire use is indicated only at 300-400 kya (Roebroeks and Villa, 2011a, 2011b), while others posit a date near the end of the Late Pleistocene, suggesting only opportunistic fire use by earlier hominins (Sandgathe et al., 2011a, 2011b). These interpretations imply that fire-making behavior was not maintained by populations moving out of Africa into colder climes during the Pleistocene. For these analysts, archaeological evidence indicating anthropogenic fire use as early as 1.6 mya (Gowlett et al. 1981; Goren-Inbar, et al. 2004 etc.) does not necessarily imply a sustained pattern of fire using behavior, but rather indicates opportunistic fire exploitation. Here, we review the arguments presented by Roebroeks and

Villa and Sandgathe et al. in light of archaeological and ethnographic evidence of human fire-making and maintenance, and suggest that the inconsistencies in archaeological fire records do not necessarily indicate a lack of ability to create and maintain fire on the part of early *Homo.* We also show that the positive benefits provided by fire control and use are such that the behavior would never have been abandoned once adopted.

3.2 Introduction

The adaptive significance of fire control in human evolutionary history is widely acknowledged, but debates about the timing of initial human fire use are ongoing. These debates are primarily rooted in the analysis and interpretation of often disparate lines of evidence nominated as indicators of human pyrotechnic ability. For example, physiological adaptations such as reduced molar size are suggested to indicate a deep antiquity of cooked food consumption in our ancestors with anatomical changes reflecting these physiological shifts appearing in the morphology of *H. ergaster/African H. erectus* ~1.8 million years ago (Burton 2009; Carmody and Wrangham 2009; Wrangham 2009; Wrangham and Carmody 2010). This "cooking hypothesis" suggests that an adaptation to eating cooked food, a consequence of fire control and use, was a primary driver of hominization during the Plio-Pleistocene transition.

While some archaeological evidence from African sites such as Koobi Fora FxJj20 East (Bellomo 1994; Rowlett 2000), Chesowanja GnJi1/6E (Gowlett et al. 1981, 1999), and Swartkrans (Brain 1993; Sillen and Hoering 1993) suggest the use of fire by genus Homo at 1.5 Ma, 1.42 $\pm$ 0.7 Ma, and 1.0-1.5 Ma, respectively, the interpretations of these archaeological data remain controversial, and their associated age ranges postdate

the morphological changes Wrangham and collaborators identify as reflecting a reliance on cooked foods. The recent analysis of intact sediments from Wonderwerk Cave, South Africa, while providing the earliest strongly suggestive archaeological evidence of controlled fire use by hominids dating to 1 million years ago (Berna et al. 2012), still does not correspond with the earliest temporal occurrence of genus *Homo* in Africa. This led Wrangham (2006) to define the discrepancy between the anatomical evidence of a reliance on cooked foods in *H. erectus* and archaeological evidence of fire use as the "cooking enigma" given the hypothesized biological consequences of cooking.

Reliance on archaeological signatures of anthropogenic fire has led many researches to conclude that strong evidence of habitual, controlled fire use does not appear until the Middle Paleolithic ~400 kya (e.g., James 1989; Straus 1989; Gamble 1993; Monnier et al. 1994; Brace 1995; Roebroeks and Villa 2011a). This has resulted in many archaeologists discounting Wrangham's cooking hypothesis; C. Loring Brace, for example, concludes that Wrangham is "on the wrong track" because the archaeological record shows that "The application of heat for food was a late thing" (Pennisi 1999: 2004). The question of "how late" has been the point of recent debate between two groups of researchers, with one group interpreting European archaeological data as evidence of habitual fire use by hominins occurring ~300-400 kya during the Middle Paleolithic (Roebroeks and Villa 2011a, 2011b), while others posit a much later date in the Late Pleistocene/Upper Paleolithic based on different data (Sandgathe et al. 2011a, 2011b). These analyses are driven by the question of whether controlled fire use was a technological adaptation habitually maintained by members of genus *Homo* as they moved out of Africa into the colder latitudes of the Old World during the Pleistocene,

and by skepticism of the long-held assumption that "the earliest evidence for fire use marks the points [sic] at which it becomes inextricably part of hominid adaptations" (Sandgathe et al. 2011b:E298).

The debate between Roebroeks and Villa and Sandgathe et al. highlights a broader issue related to understanding the evolution of human fire use: is the presence or absence of anthropogenic fire signatures in archaeological record an accurate measure of human fire-using behavior? We address this question by reviewing the arguments presented by Roebroeks and Villa and Sandgathe et al. in light of archaeological and ethnographic evidence of human fire use and maintenance and suggest that the inconsistencies in archaeological fire records do not necessarily indicate a lack of ability to create and maintain fire by early *Homo*. Furthermore, we show that the positive benefits provided by fire control and use are such that the behavior would never be abandoned despite claims of "opportunistic" fire use in the past.

3.3 The Argument for Habitual Anthropogenic Fire Use Arising During the Middle Paleolithic

Roebroeks and Villa (2011a) rank the controlled use of fire with the emergence of tool manufacture as the most significant events in human technological innovation, reinforcing its adaptive significance by stating, "most archaeologists would agree that the colonization of areas outside of Africa **[by members of genus Homo],** especially of regions such as Europe where temperatures at times dropped below freezing (Parfitt et al. 2010) was tied to the use of fire…" (p. 298). They test the strength of this assumption and the hypothesis that more extensive fire use seen in the Upper Paleolithic is part of the suite of behavioral characteristics that emerged among modern humans in

Africa and contributed to their global expansion by reviewing evidence from the European Paleolithic archaeological record (e.g., McBrearty and Brooks 2000; Brown et al. 2009).

They note that the most common fire proxies in archaeological sites "consist of various find categories that display traces of having been submitted to heating: the reddened sediments on which a fire was built, heated stone artifacts, charred bone fragments, and pieces of charcoal" (2011a:1 of 6), and consider direct (e.g., hearths) and indirect fire evidence (e.g., charcoal, heated lithics, burned bones, etc.) in their reconstruction of prehistoric fire use. Roebroeks and Villa compensate for the potential confounding effects of natural fire in the archaeological record by limiting their site samples to shelter and cave site locations. The sites they nominate as having the earliest possible evidence of fire, Beeches Pit in England and Schöningen Germany, contain heated lithics and sediments interpreted as the remains of hearths (Preece et al. 2006; Gowlett et al. 2005), and heated flints, charred wood, and possible hearths (Richter 2008; Schiegl and Thieme 2008), respectively. Roebroeks and Villa read these records as indicating a paucity of fire evidence, and therefore fire use by archaic hominids, until after 400 kya, hundreds of millennia after initial colonization of areas outside Africa. They further suggest that evidence of habitual fire use is not apparent in Europe until MIS 5 (~100 – 74 kya), and therefore "fire was not an essential component of the behavior of the first occupants of the northern latitudes of the Old World. It is only much later, with the Neanderthals and their contemporaries elsewhere in the Old World that fire became an integral part of the technological repertoire of the human lineage" (Roebroeks and Villa 2011a:5213). Roebroeks and Villa construct a European

prehistory where fire is only opportunistically employed by members of genus Homo until the rise of Neanderthals, whom they nominate as the first habitual fire users in our clade.

3.4 The Argument for Habitual Anthropogenic Fire Use Arising During the Late Pleistocene/Upper Paleolithic

Other analysts (Sandgathe et al. 2011a, 2011b) read the European record as indicating habitual fire use at a much later date near the end of the Late Pleistocene. Sandgathe et al. suggest that the pattern of increasing evidence of fire through time observed by Roebroeks and Villa may merely reflect overall site frequency per time period because the methodology they employ does not effectively quantify the proportion of sites with evidence of fire use or the levels in which fire use are apparent or absent (Sandgathe et al. 2011a:217).

Based on their recent excavations and reanalysis of archaeological evidence from Peche de l'Azé IV (Bordes 1975; Turq et al. 2008 in press) and Roch de Marsal (Sandgathe et al. 2011a; Turq et al. 2008 in press)**,** Sandgathe et al. push the date for consistent fire use closer to the present than the 300-400 kya suggested by Roebroeks and Villa. Sandgathe et al. rely on "clear charcoal and ash layers," "burned bones," "burned lithics," and "rubified sediments" as fire indicators at Peche IV, and "major concentrations of ash and charcoal, discrete charcoal and ash units, burned/calcined bone, burned lithics, and rubified sediments" (p. 222) at Roc de Marsal to reconstruct the prehistory of anthropogenic fire use in Europe, which they interpret as indicating a lack of consistent controlled fire use until the Upper Paleolithic/late Pleistocene. Contrary to Roebroeks' and Villa's conclusion that Neanderthals were fully capable of

creating and maintaining fire for 250,000 years through interglacial and full glacial periods, Sandgathe et al. contend that, "if Neanderthals had the ability to make fire at will, then evidence for it should occur with much greater frequency in Middle Paleolithic sites and occupations and especially, those sites associated with cold stages" (Sandgathe et al. 2011a).

3.5 Interpreting the Absence of Fire Evidence in the Archaeological Record

While the point of contention between the conclusions drawn by Roebroeks and Villa and Sandgathe et al. is essentially whether Neanderthals living in the colder climes of Pleistocene Europe habitually used fire, both research groups agree that the European archaeological record indicates only opportunistic fire use by archaic humans; the crux of their argument is focused only on the date when sustained, controlled fire use occurs (Roebroeks and Villa at ~300-400 kya; Sandgathe et al. ~the late Pleistocene/Upper Paleolithic). The conclusions derived from their respective analyses suggest that the habitual control and use of fire is not a distinctive characteristic of genus *Homo*, and at minimum did not occur for hundreds of millennia after migration out of Africa, contrary to several lines of evidence interpreted as indicating a long history of habitual fire control and use.

Is "the simplest explanation" (Roebroeks and Villa 2011a:5212) for the inconsistent fire signature in the European Paleolithic archaeological record that fire creation, control, and use was a transient behavioral trait for genus Homo until 300-400 kya (e.g., Roebroeks & Villa) or the late Pleistocene (e.g., Sandgathe et al.)? This explanation assumes that the absence of archaeological indicators of fire use, when compared to

accounts of fire use among contemporary hunters and gatherers, reflects an absence of the ability to create and maintain fire in the past. The logic of this assumption is encapsulated by the statement that, "Given the ubiquity of fire use among essentially all modern hunter-gatherers—fires are truly an important part of their *daily* behavior, both year round and in every environmental circumstance—then it should be ubiquitous in Mousterian occupations as well if it were a major part of their adaptation to the conditions they faced at that time" (Sandgathe et al. 2011b:220[original emphasis]).

This expectation relies heavily upon the interpretation of the absence of archaeological indicators of fire as reflecting an absence of the ability to create and maintain fire in the past. The presence or absence of pyrogenic features in archaeological strata, however, does not necessarily reflect the presence, absence, or habitualness of fire-using behavior. While Roebroeks and Villa employ this metric and logic to explain the fire signature of the European Middle Paleolithic (2011a:298), they ironically criticize the late date of controlled fire use offered by Sandgathe et al. for this very reason, noting that: "Indeed, not all Middle Paleolithic sites contain good evidence for use of fire, but this also applies to Upper Paleolithic sites, open-air as well as rock shelter ones…Again, Upper Paleolithic sites with well-preserved stratified sequences do not always have evidence of fire in all layers…Yet nobody would argue that Upper Paleolithic hunter-gatherers were not habitual users of fire."

Employing the fire-using behavior of contemporary hunter-gatherers as an heuristic analog for expectations of archaeological fire signatures further complicates the issue, since observed fire use by modern human foragers often involves no prepared hearths and leaves only ephemeral traces (Mallol et al. 2007; O'Connell et al. 1999) despite

being an omnipresent behavior.

3.6 Anthropogenic Fire Signatures in Prehistoric North America: A Comparative Example

The patterning of archaeological signals of human fire use through time in North America illustrates the inconsistent archaeological preservation of the effects of human fire use, and provides a comparative case by which to measure the strength of the conclusions presented by Roebroeks, Villa, and Sandgathe et al. about the constancy of fire creation and utilization during the Pleistocene. A survey of this pattern is found in Thoms' (2009) review of the propagation of hot-rock cookery in North America from the late Pleistocene until present, which necessarily includes a description of archaeological signatures of human fire use. Thoms (2009:577) relates that, "Hearth remains of any kind are rarely found at North American sites attributed to late-Pleistocene hunter-gatherers (Fagan 2000; Willey and Phillips 1958)," a pattern which "holds true for Paleoindian sites in the American Southeast (Anderson and Sassaman, 1996)" (Thoms, 2009:578). Furthermore, "Fire-cracked rocks are rare to absent at Paleoindian sites throughout the Great Plains (Hammatt, 1976; Reeves, 1990), as exemplified by the well-studied Blackwater Draw site in New Mexico (Hester et al. 1972), the Lindenmeier site (Wilmsen and Roberts, 1978), and the Agate Basin site in Wyoming (Frison 1991)." And, along the woodland-plains ecotone in Texas during the Paleoindian period, the "absence of any type of stone hearth is striking…(Story 1990:177)" (Thoms 2009:578).

Conservatively assuming a continent-wide human occupation dating from 13,500 to 13,350 years ago as indicated by the distribution of Clovis material culture (Fagan

2005), the paucity of archaeological evidence of anthropogenic fire use in North America until ~10,500-10,000 years ago (Thoms 2009) leaves an almost 4000 year gap in the presence of human fire signatures for the continent. Following the analytical logic employed by Roebroeks, Villa, and Sandgathe et al., this absence of evidence should reflect a behavioral inability to create and maintain fire on the part of the anatomically modern hunter-gatherers inhabiting North America that spans millennia. This explanation, however, has never been offered to account for the North American anthropogenic fire pattern (or lack thereof) during the cooler, drier climatic conditions of the Pleistocene. To paraphrase Roebroeks and Villa (2011b), no one would argue that Late Pleistocene hunter-gatherers in North America were not habitual fire users despite a lack of archaeological indicators of such behavior.

Thoms' explanation for the lack of these indicators in early North American archaeological sequences provides widely applicable insights into how different uses of fire are preserved archaeologically. His goal is explaining changes in the frequency and types of fire signatures through time, with focus on the increased use of fire cracked rock (FCR) and cook-stones characterized as "hot rocks used as heating elements in earth ovens, steaming pits, and surface griddles, as well as those used for stone boiling" in North America (2009:575). Thoms suggests that the propagation of these cooking techniques, and the archaeological fire signature created by them (e.g., macro- and microscopic evidence such as realigned magnetic particles, reddened appearance resulting from oxidation, blocky and curvilinear fragments with sharp edges, oxidized and carbon-stained sediment, charcoal, and charred food remains), is the result of land-use intensification (Binford 2001; Lourandos 1985) driven by localized population

packing.

Thoms defines land-use intensification as "a trend through the millennia toward expenditure of more energy per unit area to recover more food from the same landscape to feed more people" (2009:575). An effect of this intensification is the increased use of resources such as geophytes (e.g., bulbs, corms, tubers, and rhizomes), some of which require long cooking times to render them edible. Not all geophytes require intensive cooking, exemplified in North America by Biscuit root (*Lomatium cous*) and Yampa (*Periderida gairdneri*), but many such as Camas (*Camassia quamash*) must be cooked for up to 48 hours to sufficiently undergo the process of hydrolysis to make them edible (Thoms 1989; Thwaites 1959). Thoms hypothesizes that the intensified reliance upon these resources, and the attending increase in cooking times they require, are reflected in a more prominent fire signature observed in the archaeological record.

By linking the types of foods being consumed to the amount of processing in the form of cooking they necessitate, Thoms (2009:578) not only explains the propagation of intensive fire signatures in the North American archaeological record, but the *absence* of early fire signatures as well:

> No doubt the rarity of hearths at early Paleoindian sites reflects low population densities and poor preservation conditions for rockless cooking rather than a paucity of cooking fires per se…Judging from the dearth of cook stones at sites in western North America that date prior to 10,000 B.P., it is reasonable to conclude that Paleoindian diets focused on foods that were easily cooked on, above, or in a bed of hot coals prepared on the ground surface or in a shallow depression. Lean meat and fish, for example, cook quickly on coals and an abundance of ethnohistorical data attests to a variety of geophytes being cooked on/in coals (Thoms, 2006, 2008b; Wandsnider, 1997).

Furthermore,

> By the late Pleistocene, hot-rock cookery was well developed in the Old World but at the same time in the New-World food was prepared almost exclusively in

> rockless cooking facilities…That neither the newcomers nor their descendants for several millennia used cook stones regularly enough to render them archaeologically visible is consistent with the working model presented here. As per the model's primary theoretical tenet, propagation of hot-rock cookery is triggered by population packing, which is measured in terms of a given region's food-resource potential relative to its extant land-use system (Binford 2001). Easily cooked foods, including lean meat and starch-rich geophytes, along with nuts and fructose-rich berries and fruits, were readily available to the earliest occupants of the new land. There was little to compel them to systematically invest ostensibly leisure time in the comparative drudgeries inherent in cook-stone technology (p. 588).

3.7 Subsistence Transitions, Widening Diet Breadth, and Fire Signature Visibility in the Archaeological Record

Thoms' model explaining the increased frequency of visible archaeological evidence of fire use through time in North America as a consequence of resource intensification echoes predictions generated from optimal foraging models regarding subsistence transitions (Hawkes and O'Connell 1992). Using the "optimal diet model" (Emlen 1966; MacArthur and Pianka 1966), Hawkes and O'Connell highlight how the link between diet breadth and time allocated to either search or handling has important implications for understanding changes in subsistence-related behavior. The optimal diet model assumes an individual forager's goal is to maximize net rate of energy intake, and poses the foraging decision as a single, repetitive, yes/no choice that depends on the probability of encountering an alternative resource with a higher return rate. The *currency* through which this goal is measured is typically specified as rate of energy acquisition (kcal/hr). The model partitions total foraging time into two mutually exclusive aspects of foraging: *search* and *handling*, and assumes that resources are encountered randomly relative to their abundance, and that foragers can accurately estimate likely encounter and post-encounter return rates for all potential prey items

(i.e., "complete information"). Search is the time it takes to locate a resource, and is generalized across all resources. All time spent pursuing, processing, and extracting energy from that resource after encountering it is considered handling. Resources are then ranked by their expected net profit of energy per unit of time spent in handling (postencounter return rate). Highest ranked resources are always included in the optimal diet with lower-ranked resources added or dropped in order of profitability depending on encounter rates with higher ranked resources.

When diets are narrow, more time is devoted to search. As a consequence, improvements in search efficiency should be favored to increase encounter rates with profitable food types. Conversely, broader diets (i.e., those that include more lower-ranked resources) require that significant time be devoted to *handling*; under these conditions, improvements in handling efficiency will have the greatest effect. Such innovations should be adopted by rate maximizing foragers where diets are already broad, because that is the *only* way to achieve higher energy acquisition rates under these conditions.

Cooking (i.e., chemically altering a resource through the application of fire) can be viewed as a handling improvement because reductions in chewing effort (Dominy et al. 2008), and chemical alterations that increase digestive efficiency (Carmody and Wrangham 2009; Oka et al. 2003) lower handling, or postencounter processing costs. For example, fire treatment improves the digestibility of proteins found in seeds and nuts (Kataria et al. 1989) and the digestibility of underground storage organs by neutralizing toxicity (Carmody and Wrangham 2009) and gelatinizing starchy tissues (Wansnider 1997). Cooking also increases the fracture rate for some tubers by 49%

(Dominy et al. 2008). Cooked meat is also easier to chew and digest because tough tissues have been denatured (Waldron and Smith 2003). All of these alterations make the nutrients in these resources more readily available and accessible, reducing post-encounter handling efforts that raise prey profitability and ultimately result in higher return rates.

Cooking improves handling efficiency so effectively in some cases it changes the prey type of resources within the optimal diet. Recall that the optimal diet model ranks resources by their expected net profit of energy per unit of time spent in handling. If this postencounter return rate increases, i.e., the nutrients in said resource can be extracted and utilized more efficiently, the ranking of that resource in the optimal diet improves. When cooking increases the bioavailability of nutrients that can be extracted from a resource via chemical and/or mechanical alteration, the handling cost of that resource is reduced. A cooked tuber, for example, will be a different prey type within the framework of the optimal diet model than an uncooked tuber, despite taxonomically being the "same" resource; cooking changes the postencounter profitability of the tuber by reducing its processing cost.

Cooking changes the profitability of some resources so significantly, it is the only way they can be consumed. Camas (*Camassia quamash*), which requires extensive cook-times to become edible, exemplifies the power of cooking as a handling innovation. It also highlights the relationship between the inclusion of lower ranked resources into the diet and the amount of time that must be allocated to processing them, as noted by Hawkes and O'Connell (1992). Given that cooking is such a broadly applicable method of handling resources, it stands to reason that lower ranked resources

will require more intensive handling effort, taking the form of longer cooking times and longer burning fires in this case. The remnants of such fires will be more substantial than those which burn quickly, resulting in a higher likelihood of being preserved archaeologically as Thoms shows in the North American record. Increased archaeological fire signatures, therefore, are likely indicators of longer burning, more intense fires, perhaps reflecting increased cooking times for lower ranked resources. Alternately, fires which burn quickly are less likely to leave an archaeological signature.

3.8 Explaining the Difference in Neanderthal versus Anatomically Modern Human Fire Signatures

Much of the debate over the degree of fire maintenance by Middle Paleolithic Neanderthal populations may be instigated, in part, by the marked difference in the archaeological fire signature associated with anatomically modern humans during the extreme climatic conditions of the last glacial cycle of the European Upper Paleolithic (Thery-Parisot 2002). Differences between Upper Paleolithic and Mousterian archaeological records have often been interpreted as reflecting fundamental differences in the adaptive capacities of anatomically modern humans as compared to Neanderthals (e.g., Mellars 1996; Stringer and Gamble 1993). The features of the Upper Paleolithic archaeological record--the exploitation of a wider array of food resources and habitats, more complex and diverse toolkits, ornamentation, art, and more extensive fire use--are all seen as markers of uniquely modern human symbolic and cognitive capabilities. This greater "capacity for culture" is suggested to be the adaptive behavioral advantage which facilitated the expansion of anatomically modern humans out of Africa and the subsequent displacement of populations of archaic hominids (including Neanderthals)

throughout the Old World. Analysis of ancient DNA, including a draft sequence of the Neanderthal genome, however, implies a pattern of interaction and interbreeding between moderns and archaics in the Levant (Green et al. 2010) and East Asia (Reich et al. 2011) as moderns migrated out of Africa and into Pleistocene Australia/New Guinea.

Contrasts observed between the Mousterian and Upper Paleolithic archaeological records may instead be due to differences in population density and resource acquisition. O'Connell (2006) constructs a speculative model in which population growth of moderns in Africa prior to 50kya (Rogers 1995) entailed an escalation in the cost of subsistence and a broadening of the diet to include lower-ranked resources, archaeologically indicated by an increase in technological complexity and the habitation of more diverse environments (McBrearty and Brooks 2000). As populations of anatomically modern humans rapidly expanded out of Africa, going East to Sahul (Pleistocene Australia/New Guinea) and North into Europe, their larger populations, broader diets necessitating more complex processing technology, and lower energy budgets provided a competitive advantage over Neanderthals with relatively narrow diets inhabiting Europe at the time. Moderns essentially "outcompeted" Neanderthals by taking a wider array of resources, including those upon which Neanderthals were entirely dependent.

This model has direct implications for the understanding the archaeological fire signature associated with moderns in the Upper Paleolithic, and allows for the generation of hypotheses to explain the observed pattern. As noted above, lower ranked resources generally require more extensive processing (Hawkes and O'Connell 1992), including longer cooking times and investment in hearth construction (Thoms 2009).

The stronger Upper Paleolithic fire signature is likely a reflection of this. As O'Connell notes, "The fact that early Upper Paleolithic moderns routinely operated under much more rigorous circumstances implies increased investment in critical technology, **e.g. more efficient hearths** and better clothing and shelter" (O'Connell 2006:51, emphasis added).

3.9 Ethnographic Examples of 'Fire Loss'

To support their contention of transient fire-making and maintenance behaviors prior to the Upper Paleolithic, Sandgathe et al. emphasize the ease with which contemporary hunter-gatherers start fires (Mallol et al. 2007:2), and use the wide range of fire use described among historic hunter-gatherers as the gauge by which to measure the intensity and frequency of fire use the Mousterian (2011b:217-218). Conversely, they also rely on ethnographic descriptions of "fire loss" to support their hypothesis that "Neandertals did not know how to make fire" but instead opportunistically maintained fires ignited by natural processes (p. 235), with the caveat that that this conclusion "has no implied relation to differences in cognitive abilities between Neanderthals and modern humans" (p. 237).

Accounts of a loss of fire-making knowledge among hunter-gatherers appear to support the idea that pyrotechnical knowledge can be lost, abandoned, or is a tool of transient utility, and have been used to exemplify the expectations of cultural group selection models (Boyd and Richerson 1996;1985) and "cultural transmission theory" (Heinrich 2001). For example, the description of Northern Ache losing the ability to make fire cited by Sandgathe et al. is employed in its original context to illustrate the how the loss of cultural innovation can occur due to the lack of large interaction

networks in small populations (Hill et al. 2010:1288). Similarly, reports of Aboriginal Tasmanians lacking the ability to make fire have been used as supplementary evidence to support the explanation of a reduction in technological complexity over time due to geographic isolation and small population size (Heinrich 2004:213, Note no. 2; Jones 1977).

Close examination of these accounts, however, suggests that the inferences drawn from them regarding the impermanence of fire-making and control within the human behavioral repertoire are not the only ones that can be made. The Northern Ache, Tasmanian, and Yuqui (Stearman 1991; also cited by Sandgathe et al.) accounts all rely upon salvage ethnography, oral history, or second hand historical accounts to establish a loss of fire-making ability rather than first hand observation of the phenomenon.

The moist rainforest environments inhabited by Yuqui, Northern Ache, and Tasmanian hunter gatherers significantly increase the challenge of making fire, and tales of losing the ability to do so in the past may in fact be didactic rather than descriptive. Gott's review of evidence for the persistent claim of loss of fire making ability among the Tasmanians leads her to conclude that:

> Fire-making was difficult in the damp Tasmanian climate, and the preference was to carry fire from place to place, but the Tasmanians did know how to make fire. Fire-making may have been a skill possessed only by certain members of the group. Making fire by percussion seems to have been limited to an area of southern Tasmania around Bruny Island. The fire-plough was the most likely other method of firemaking, and the drill method is the one most likely to have been acquired from mainland sources (Gott 2002:655).

It is likely, then, that the environmental similarities in the cases noted above led the hunting and gathering inhabitants of these damp environments to focus more on the

necessity of *preserving* rather than making fire, an emphasis that would be highlighted in oral histories of precontact life. It is important to note that in none of these ethnographic cases, or others where tales of a loss of fire-making ability are recorded (e.g., Holmberg 1950; Oswalt 1973), has a loss or absence of fire use been observed; ultimately, there are no "people without fire" in the ethnographic record.

3.10 Discussion

Analysts of the European Paleolithic archaeological record have interpreted gaps in the archaeological fire signature of hominids inhabiting the region during that time period as indicating a transitory ability to create and maintain fire. They suggest that fire exploitation for our genus was merely opportunistic and contingent upon natural pyrogenesis from lightening until ~300 to 400 kya (Roebroeks and Villa 2011a; 2011b) or the Late Pleistocene/Upper Paleolithic (Sandgathe et al. 2011a, 2011b). These interpretations are based on several assumptions: that the fire signature of archaic hominins should be more pronounced if fire use was as ubiquitous for them as modern hunter gathers; that the archaeological signature of fire use should be more prevalent during cold periods; that the absence of evidence for fire use in the archaeological can be reliably interpreted as an absence of the ability to create and maintain fire by our evolutionary ancestors; and that support for this assumption can be found in ethnohistorical accounts of populations losing the ability to create and maintain fire using behaviors.

While The point of contention between these archaeologists is whether Neanderthals (Roebroeks and Villa 2011a, 2011b) or anatomically modern humans were the first habitual users of fire in our genus (Sandgathe et al. 2011a, 2011b), they share

skepticism as to whether "the earliest evidence for fire use marks the points at which it becomes inextricably part of hominid adaptations" (Sandgathe et al. 2011a). We suggest that the long-held assumption about human evolution challenged by Roebroeks and Villa and Sandgathe et al. that when fire begins to be used "it becomes inextricably part of hominin adaptations," (Sandgathe et. al, 2011a) is sound, for the very reason its critics themselves acknowledge: fire use provides significant adaptive advantages including warmth, light, and cooking. Hypotheses suggesting that fire control and use could be transient behaviors for our genus underestimate the significance of the advantages fire provided our evolutionary ancestors. We instead argue that these advantages were so significant that they changed the selective pressures on our genus, resulting in Homo being an actively pyrophilic primate dependent on fire for its survival. We agree that a critical assessment of the importance of fire use in our genus is warranted, but we suggest that this sentiment be directed toward understanding the extent to which fire control and use changed the selective pressures on our genus, rather than suppositions of opportunistic fire use based on interpretations of localized archaeological records.

Interpreting the inconsistent signature of human fire use in archaeological records as evidence of inconsistent fire control and use in the behavioral repertoire of prehistoric populations can be criticized for the reasons listed above. Evidence from North America shows how an absence of fire signatures in the archaeological record created by fully modern humans does not indicate an absence of capacity for fire creation and maintenance, and how obvious fire signatures in the archaeological record indicate much more about the amount of processing via fire treatment a resource requires.

Concomitant to this, it is important to note that while the most common archaeological indicators of anthropogenic fire are hearths, not all hearths are used for cooking and not all cooking is done in hearths. Ethnographically known hunter-gatherers often cook foods over fires that leave no archaeological remnant, and the widely observed practice of low-intensity small-scale landscape burning (see Bird et al. 2005; Bliege Bird et al. 2008; Keeley 1999) cannot be differentiated from natural fires in the archaeological record. We agree that the evidence presented by both Roebroeks and Villa and Sandgathe et al. indicate a counterintuitive archaeological signature of fire use during cold periods in the Middle Paleolithic of Western Europe, but suggest that this pattern may be better explained in terms of variation in the conditions under which fire-use signatures enter into the archaeological record and the degree to which they are preserved (see Malol et al. 2010), rather than being a reflection of opportunistic or transient fire using behavior among archaic hominins. One avenue of research that would likely help illuminate this problem would be to conduct ethnoarchaeological experiments into how the fires used by contemporary hunter-gatherers living in high latitudes are reflected in the archaeological record.

The question of when fire use and control would ever be abandoned once integrated into the behavioral repertoire of members of our genus can be asked more directly in light of assertions of "opportunistic" fire use based on interpretations of evidence (or lack thereof) from a localized archaeological record that by its nature is an imprecise and incomplete reflection of hominin behavior. Under what conditions would the abandonment of fire control and use would be reasonably expected in light of evidence indicating earlier pyrotechnical behavior by genus *Homo?* Once our evolutionary

ancestors created and maintained fire, why would that behavior ever be abandoned in favor of “opportunistic” fire use?

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